

**ENIGMATIC TREEHOPPER GENERA (HEMIPTERA: MEMBRACIDAE):
DEIRODERES RAMOS, *HOLDGATIELLA* EVANS, AND *TOGOTOLANIA*,
NEW GENUS**

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Abstract—Two poorly known Neotropical treehopper genera, *Deiroideres* Ramos and *Holdgatiella* Evans, are revised and redescribed based on adult morphology. The Caribbean genus *Deiroideres* (unplaced within the subfamily Stegaspidae) has three valid species including *D. inornatus*, **new species** (Jamaica). The Neotropical genus *Holdgatiella* (currently unplaced within Membracidae) has two valid species including *H. stria*, **new species** (Venezuela). In addition, a previously unknown Caribbean genus is here described, *Togotolania*, **new genus**, with two species: *T. longicornis*, **new species** (Dominican Republic) and *T. brachycornis*, **new species** (Guadeloupe). All species included in these three genera are illustrated, and keys are given for the identification of adults.

Key Words: Membracidae, *Deiroideres*, *Holdgatiella*, *Togotolania*, Caribbean, taxonomy

Treehoppers (Hemiptera: Membracidae) are traditionally recognized by the enlarged pronotum, which in many species is conspicuously ornamented with stalks, spikes, or bulbs. In most genera, there is at least a posterior pronotal process extending over (or even concealing) the scutellum. However, the pronota of the Neotropical treehopper genera *Deiroideres* Ramos and *Holdgatiella* Evans are remarkably unremarkable. A third genus, *Togotolania*, described here as new, also has a simple pronotum, adorned only with a median horn. These three genera are probably not closely related, indicating that enlarged pronotal ornamentation was likely gained or lost multiple times in Membracidae. Other treehopper genera lacking a posterior pronotal process occur in the subfamilies Nicomiinae, Endoiastinae, Centrotinae, and Stegaspidae (fossils), though these may be cases of secondary loss.

Following the most recent reclassifications of Membracidae (Deitz and Dietrich 1993a, Dietrich et al. 2001a), *Deiroideres* and *Holdgatiella* were among several genera that remained unplaced within the taxonomic framework. Although these two genera were originally described in the subfamily Centrotinae (Ramos 1957a, Evans 1962a), emerging morphological (Dietrich et al. 2001a, Cryan et al. in press) and molecular (Cryan et al. 2000a, Cryan, unpublished data) evidence is revealing support for new phylogenetic placements within Membracidae, as discussed below.

MATERIALS AND METHODS

Protocols used during this work follow the materials and methods described by Cryan and Deitz (1999a). The following codens are used to refer to the collections in which relevant specimens are located or

have been deposited. Arnett et al. (1993a) listed the full postal addresses for most of the institutions; those not found in that publication are indicated by a dagger (†) following the coden.

CIRAD†: Labo Entotop (Faunistique-Taxonomie), Montpellier, France.

CNCI: Canadian National Collection of Insects, Agriculture and Agri-Food Canada, Ottawa, Canada.

JARC†: J.A. Ramos Collection, University of Puerto Rico, Mayagüez, Puerto Rico.

JWEC†: J.W. Evans Collection, c/o Australian Museum, Sydney, Australia.

MNHN: National Collection of Insects, Muséum National D'Histoire Naturelle, Paris, France.

NCSU: North Carolina State University Insect Collection, Department of Entomology, North Carolina State University, Raleigh, North Carolina, USA.

SHMC†: S.H. McKamey Collection; current address: Systematic Entomology Laboratory, USDA, % National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560-0168, USA.

USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Genus *Deiroderes* Ramos 1957

Deiroderes Ramos 1957a: 96. Type species: *Deiroderes inermis* Ramos 1957a: 96, by original designation.

Diagnosis.—The genus *Deiroderes* includes small stegaspidine treehoppers with simple pronota (lacking well-developed suprahumeral horns and posterior pronotal process) and dark tubercles along the veins of the forewings.

Adult.—*Dimensions* (mm): total length (from head to apex of forewings at rest) 3.2–3.9. *Structure: Head* (Figs. 1–2, 8–9, 14–15): broad, wider than long, with fine pubescence; ocelli not raised, above centro-ocular line; foliate lobes small, rounded or quadrate; postclypeus weakly or strongly

trilobed. *Thorax: Pronotum* (Figs. 2, 9, 15): simple, convex; either low or elevated; suprahumeral horns represented by low carinae, or absent; posterior pronotal process absent. *Pronotal surface sculpturing*: finely punctate, each pit associated with one short seta; setae clubbed, normal, or flattened. *Scutellum* (Figs. 2, 9, 15): short, acuminate; anterior half slightly raised; posterior half flattened, with slight median depression. *Legs* (Figs. 3, 10): metathoracic femur with or without dorsal row of cucullate setae; metathoracic tibia with enlarged setal rows I, II, and III, all with cucullate setae; metathoracic tarsomere I with 1 apical cucullate seta. *Forewing* (Figs. 4, 11, 16): punctate, coriaceous basally; venation simple; 1 [rarely, 2] r-m and 1 m-cu crossvein present; dark tubercles, each bearing one stout seta, spaced irregularly along veins and crossveins. *Hindwing*: venation essentially identical to *Microcentrus* hindwing venation as illustrated by Deitz (1975a, fig. 37c) and Dietrich et al. (2001a, fig. 2B). *Genitalia*: ♀ 2nd valvulae (Figs. 5, 17) narrow throughout, with distinct dorsal serrations; ♂ lateral plates (Figs. 6, 12) free, without hook; aedeagus and styles (Figs. 7, 13) variable; aedeagus with anterior face of posterior arm not denticulate.

Range.—Caribbean, from Virgin Islands to Cuba.

Remarks.—Ramos (1957a) originally described *Deiroderes* as a member of the subfamily Centrotinae, indicating the genus was closely related to *Lophyraspis* Stål (now in Aetalionidae: Biturritiinae: Biturritiini) and *Tolanía* Stål (now in Membracidae: Nicomiinae: Tolaniini). *Deiroderes* was later removed from Centrotinae and considered unplaced within Membracidae (Deitz and Dietrich 1993a). Dietrich et al. (2001a) found that *Deiroderes* was included within a monophyletic Stegaspidinae in some of the most-parsimonious cladograms resulting from a more detailed morphology-based phylogenetic analysis of the family Membracidae. Nevertheless, evidence for placement of *Deiroderes* remained equivocal.

cal, and therefore the genus remained unplaced in Membracidae.

In a phylogenetic analysis of basal treehopper groups, Cryan et al. (in press) found that *Deiroderes* groups with the genus *Antillotolania* Ramos at the base of Stegaspidinae. Morphological features that placed the genus within Stegaspidinae included the forewing's distal m-cu crossvein (fused basad of the fork of vein M) and hooklike apex of the male styles.

Within Stegaspidinae, some features—forewing with one r-m and one m-cu crossvein; vein R_{2+3} fused basally with R_1 ; and male lateral plates free, lacking posteroapical hooks—suggest that *Deiroderes* is more closely related to the tribe Stegaspidini (reviewed in Cryan and Deitz 1999a, b, 2000a). Nevertheless, phylogenetic analyses based on morphological (Dietrich et al. 2001a, Cryan et al. in press) and molecular (Cryan et al. 2000a, Cryan, unpublished data) evidence suggest either that *Deiroderes* might be more closely related to Microcentrini or that placement is equivocal. Therefore, pending more definitive resolution, we refer *Deiroderes* to Stegaspidinae but propose that the genus remains unplaced to tribe.

When creating a generic name that refers to a feature of the prothorax, it is customary to modify the Greek noun “*dere*” to “*deres*,” thereby making the name masculine (G. Kuschel, personal communication). The first part of the compound name, “*deiro-*,” means to behead something, or to cut the neck; thus, “*Deiroderes*” best translates as the “beheaded” treehopper, probably referring to either the lack of pronotal horns or the relatively flat head.

KEY TO THE SPECIES OF ADULT *DEIRODERES*

1. Forewing vein M branching at, or immediately distad of, crossvein r-m, M_{3+4} extending posteriorly at right angle to M (Fig. 4); metathoracic femur with dorsal and ventral rows of cucullate setae (Fig. 3) *D. inermis* Ramos
- Forewing vein M branching distinctly distad of crossvein r-m, M_{3+4} extending obliquely to

- wing margin (Figs. 11, 16); metathoracic femur without rows of cucullate setae (Fig. 10) . . . 2
2. Pronotal metopidium produced dorsally, with well-developed median carina; pronotum with suprahumeral carinae (Fig. 15)
 *D. punctatus* (Metcalf and Bruner)
 - Pronotal metopidium low, dorsal median carina not well developed; pronotum without suprahumeral carinae or horns (Fig. 9)
 *D. inornatus*, new species

Deiroderes inermis Ramos (Figs. 1–7)

Deiroderes inermis Ramos 1957a: 96.

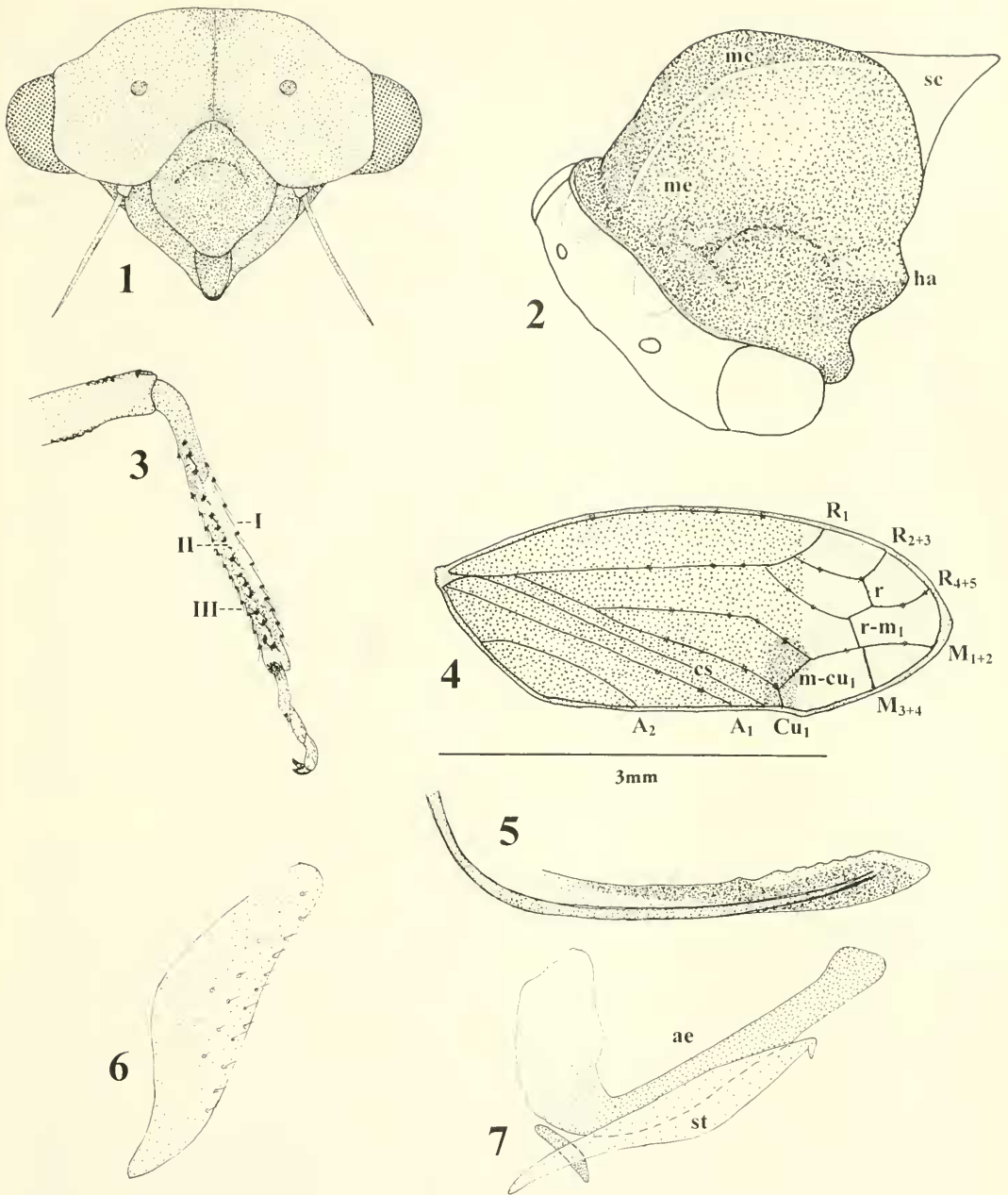
Type locality.—Guánica, Puerto Rico.

Diagnosis.—*Deiroderes inermis* has the forewing with vein M branching immediately distad of the r-m crossvein, M_{3+4} extending directly to the posterior margin of wing (nearly forming a right angle with M).

Adult.—*Dimensions* (mm): total length ♀ 3.2–3.5, ♂ 3.5; width between humeral angles ♀ 1.2–1.4; ♂ 1.3; pronotal length ♀ 0.8–1.0, ♂ 0.9; wing length ♀ 2.6–2.8, ♂ 2.4; width of head including eyes ♀ 1.1–1.3, ♂ 1.2. *Coloration*: body tan to dark brown; forewing dark basally, dark coloration sometimes extending $\frac{2}{3}$ of wing length, with dark spot at distal end of vein Cu. *Structure: Head*: dorsal projections (Fig. 1) indistinct. *Thorax: Pronotum* (Fig. 2): metopidium low; humeral angles short, blunt; middorsal crest weakly produced; suprahumeral horns and carinae absent. *Legs* (Fig. 3): metathoracic femur with dorsal and ventral rows of cucullate setae; metathoracic tibiae with cucullate setae row I less robust than setae in II or III. *Forewing* (Fig. 4): M branching immediately distal to r-m crossvein, M_{3+4} extending to posterior edge of wing, at right angle to M. *Genitalia*: ♀: 2nd valvulae (Fig. 5) narrow throughout, apical $\frac{1}{3}$ with distinct dorsal serrations. ♂: lateral plates (Fig. 6) free, lacking hooks, sparsely setose; styles (Fig. 7) with small hook apically; aedeagus (Fig. 7) with posterior arm straight.

Nymph.—Unknown.

Distribution.—British Virgin Islands: Guana Island [NCSU], Virgin Gorda



Figs. 1-7. *Deiroderes inermis*. Structures of the holotype (male genitalia illustrated from a non-type specimen). 1, Head, anterior aspect (face). 2, Head, pronotum, and scutellum, anterolateral aspect. 3, Left metathoracic femur, tibia, and tarsus, ablatral aspect. 4, Right forewing. 5, Female second valvulae, lateral aspect. 6, Male left lateral plate, lateral aspect. 7, Male aedeagus and left style, lateral aspect (illustrated with connective tissue). Abbreviations: A_n , anal vein(s); ae, aedeagus; Cu_n , cubital vein(s); cs, claval suture; ha, humeral angles; $m-cu_n$, medial-cubital crossvein(s); M_n , medial vein(s); mc, median carina; me, metopidium; sc, scutellum; st, style; r, radial crossvein; $r-m_n$, radial-medial crossvein(s); R_n , radial vein(s); I, II, III, enlarged setal rows.

[NCSU], Tortola [NCSU]; U.S. Virgin Islands: St. John [JARC]; Puerto Rico [NCSU].

Material examined.—Holotype [♀] [NCSU, deposited on indefinite loan to USNM] with labels: "Insular Forest/Guanica P.R./3-Aug. 1945./On *Capparis nitida*." "J.A. Ramos/Collector." "Holotype." "Deiroideres/inermis Ramos/145." Paratype [♀; forewings missing] [NCSU] with labels: "Cambalache/P.R. 11-7-47." "Caldwell &/Martorell/Collectors." "Paratype." "Deitz Research/83-227e ♀." "JARC." and "PARATYPE/Deiroideres/inermis/Ramos." Other specimens: 1 ♀ (Deitz Research #83-227f ♀) from JARC; 2 ♂ (Cryan Research #94-286a ♂ and Cryan Research #94-273b ♂) from NCSU; 1 ♀ from USNM.

Remarks.—The holotype of *D. inermis* was collected on *Capparis* sp. (Capparaceae), though there is a discrepancy concerning the host species. In the original description of *D. inermis* (Ramos 1957a), the holotype is listed as "on *Capparis indica* (L.) Fawc and Rendle"; however, the holotype label information indicates the host as *C. nitida* (*C. indica* and *C. nitida* are not synonyms). This insect's Latin specific epithet translates directly to "unarmed" or "weaponless," presumably referring to the complete absence of pronotal projections (suprahumeral horns and posterior process).

A specimen of *D. inermis* from the British Virgin Islands was included in a molecular systematic investigation of membracid relationships (Cryan et al. 2000a). Results based on parsimony and maximum likelihood analyses of DNA nucleotide sequence data from two nuclear genes (EF-1 α and 28S rDNA) indicated that *Deiroideres* was a member of a clade that also included *Antillotomania* Ramos and *Microcentrus* Stål.

***Deiroideres inornatus* Cryan and Deitz,
new species
(Figs. 8–13)**

Type locality.—Jamaica.

Diagnosis.—*Deiroideres inornatus* has a

simple, unadorned pronotum, strongly deflected postclypeus and beak, and sinuate aedeagus.

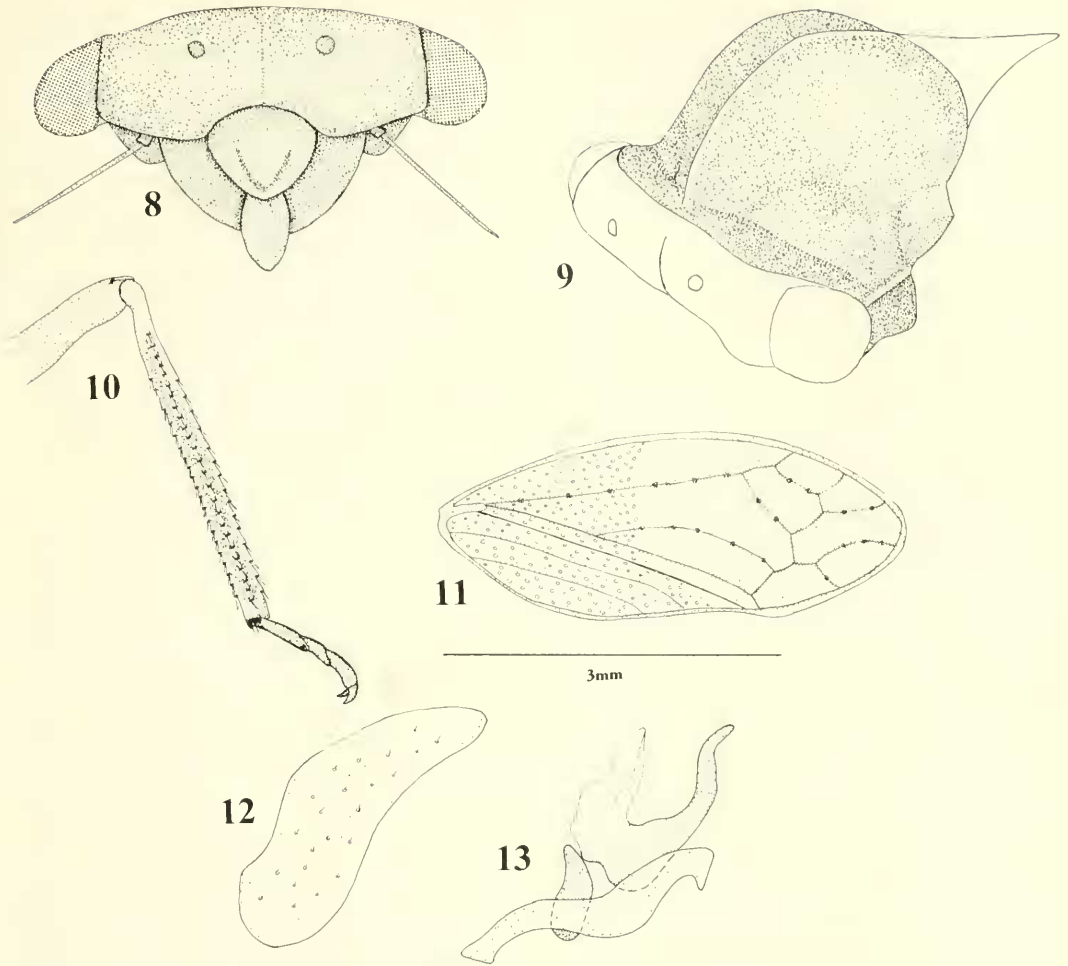
Adult ♂.—*Dimensions* (mm): total length 5.1–6.0; width between humeral angles 1.9–2.1; pronotal length 1.4–1.5; wing length 4.0–4.9; width of head including eyes 2.1–2.3. *Coloration*: body tan to dark brown; forewing tan or dark brown basally, light brown apically. *Structure: Head*: dorsal projections (Fig. 8) small or indistinct; postclypeus and anteclypeus strongly deflected under thorax. *Thorax: Pronotum* (Fig. 9): metopidium low; humeral angles weakly produced; mid-dorsal crest weakly produced; suprahumeral carinae and horns absent. *Legs* (Fig. 10): metathoracic femur without rows of cucullate setae. *Forewing* (Fig. 11): vein M branching well after r-m crossvein; M₃₊₄ extending obliquely to posterior margin of wing; some specimens with 2 r-m crossveins on one or both forewings. *Genitalia*: lateral plates (Fig. 12) free, without hooks; styles (Fig. 13) sinuate, hooked apically; aedeagus (Fig. 13) with posterior arm sinuate, narrowing apically. ♀: unknown.

Nymph.—Unknown.

Distribution.—Jamaica [USNM, CNCI].

Material examined.—Holotype [♂] [USNM] with labels: "Jamaica/19-VII-35." "Sta 16/Chapin and/Blackwelder." "Voucher Specimen/Cuticular Hydrocarbon/Analysis Study/Jason R. Cryan, 1995." and "HOLOTYPE ♂/*Deiroideres/inornatus*/Cryan & Deitz." Paratype [♂] [CNCI] with labels: "JAMAICA, 4000'/Hardwar Gap/VII-23-1966/Howden & Becker." "Specimen data/captured—NMNH/Biota (Colwell) file." and "PARATYPE ♂/*Deiroideres/inornatus*/Cryan & Deitz." Paratype [♂, dissected; head and pronotum missing] [USNM] with labels: "Jamaica/19-VII-35." "Sta 16/Chapin and/Blackwelder." "CRYAN RESEARCH/#94-273a ♂." and "PARATYPE ♂/*Deiroideres/inornatus*/Cryan & Deitz." Other specimens: 1 ♂ from CNCI; 1 ♂ from USNM.

Remarks.—*Deiroideres inornatus* is de-



Figs. 8–13. *Deiroderes inornatus*. Structures of the holotype. 8. Head, anterior aspect (face). 9. Head, pronotum, and scutellum, anterolateral aspect. 10. Left metathoracic femur, tibia, and tarsus, ablatral aspect. 11. Right forewing. 12. Male left lateral plate, lateral aspect. 13. Male aedeagus and left style, lateral aspect (illustrated with connective tissue).

scribed from five males; females are unknown. Minor color variation is evident among males, and while some specimens have 2 r-m crossveins in one or both forewings, no other substantial variation in morphology of males is apparent. Further, although some species in the subfamily Stegaspidae exhibit sexual di- or polymorphism (Cryan et al. in press), both sexes of *D. inermis* are morphologically similar. This fact, combined with the apparent allopatric distribution of *Deiroderes* species, makes it unlikely that *D. inornatus* is ac-

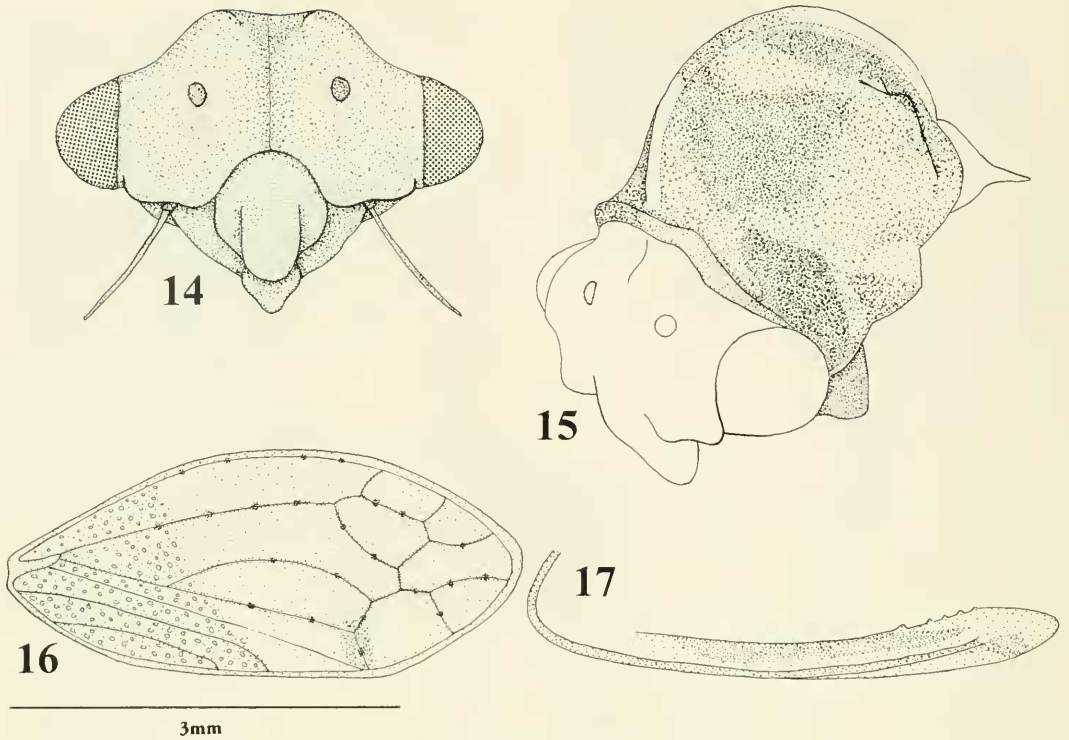
tually the male of *D. punctatus* (for which males are unknown).

The specific name “*inornatus*” is Latin for “unadorned,” referring to the lack of suprahumeral horns and posterior pronotal process in this species.

Deiroderes punctatus
(Metcalf and Bruner)
(Figs. 14–17)

Tolanina punctata Metcalf and Bruner
1925b: 213.

Eustollia punctata: Goding 1926a: 105.



Figs. 14–17. *Deiroderes punctatus*. Structures of a female paratype. 14, Head, anterior aspect (face). 15, Head, pronotum, and scutellum, anterolateral aspect. 16, Right forewing. 17, Female second valvulae, lateral aspect.

Deiroderes punctatus: Ramos 1957a: 96.

Microcentrus punctata: Hamilton 1971b: 235.

Type locality.—Camaguey, Cuba.

Diagnosis.—*Deiroderes punctatus* has an elevated pronotum with an expanded mid-dorsal carina and suprahumeral ridges.

Adult ♀.—*Dimensions* (mm): total length 3.6–3.8; width between humeral angles 1.3–1.4; pronotal length 0.9–1.1; wing length 3.0–3.1; width of head including eyes 1.3–1.4. *Coloration*: body light brown; pronotum with dark brown patches; forewing brown in basal 1/3, with dark spot at distal end of vein Cu. *Structure: Head*: dorsal projections (Fig. 14) distinct, partially hidden by anterior pronotal shelf; post-clypeus prominent, trilobed. *Thorax: Pronotum* (Fig. 15): metopidium elevated; suprahumeral carinae present; middorsal carina strongly elevated; supraocular

callosities evident. *Legs*: metathoracic femur without rows of couclate setae. *Forewing* (Fig. 16): vein M branching well beyond r-m crossvein; M_{3+4} extending obliquely to posterior margin of wing. *Genitalia*: ♀: 2nd valvulae (Fig. 17) narrow throughout, distal 1/3 with distinct dorsal serrations. ♂: unknown.

Nymph.—Unknown.

Distribution.—Cuba [NCSU].

Material examined.—Paratype [♀, dissected] [NCSU] with labels: “Camaguey, Cuba/Col. J. Acuna/Julie 15, 1923.” “On/“Guaitajan,” “190b,” “CUBA/5,” “Paratype,” “Deitz Research/73-107c ♀,” “Tolania/punctata/Metc. & Brun./det. Z.P.M.,” and “*Deiroderes/punctata*/(Metcalf & Bruner)/det. L.L. Deitz 1983.” Paratype [♀] [NCSU] with labels: “9061,” “Camaguey, Cuba/Col., J. Acuna/Julie 15, 1923.” “Paratype,” and “*Tolania/punctata*/(Metc. & Brun./det. Z.P.M.”

Remarks.—Although included in four different genera by four different authors, the overall morphology of *D. punctatus* (especially of the forewing) places it in the genus *Deiroideres*. The specific epithet is an adjective and must agree in gender with *Deiroideres* (masculine); thus the correct spelling is *D. punctatus*. Other than the cryptic reference of one specimen being found “on Guaitajan” (see Material Examined, above; we found no reference to this in any botanical literature consulted), no information is available concerning the life history, ecology, or behavior of this species.

Genus *Holdgatiella* Evans 1962

Holdgatiella Evans 1962a: 515. Type species: *Holdgatiella chepuensis* Evans 1962a: 516, by original designation.

Diagnosis.—The forewing of *Holdgatiella* has vein M 3-branched; the male aedeagus is tentaculate.

Adult.—*Dimensions* (mm): total length (from head to apex of forewings at rest) 6.1–7.9. *Structure: Head* (Figs. 18, 25): dorsal projections weakly developed. *Thorax: Pronotum* (Figs. 19, 26): suprahumeral horns and posterior process absent; metopidium steeply declivous. *Pronotal surface sculpturing*: finely punctate, each pit associated with one short seta. *Scutellum* (Figs. 19, 26): swollen basally, flattening to acuminate apex. *Legs* (Figs. 20, 27): metathoracic tibiae with cucullate setae in rows I, II, and III; metathoracic tarsomere I with 1 apical cucullate seta. *Forewing* (Figs. 21, 28): apical limbus broadened proximally along costal margin, vein M with 3 branches, 1 r-m crossvein present (distad of first branch of vein M). *Hindwing*: venation essentially identical to *Microcentrus* hindwing venation as illustrated by Deitz (1975a, fig. 37c) and Dietrich et al. (2001, fig. 2B); apex with arcuate chaetoids (Dietrich and Deitz 1993a, Dietrich et al. 2001a). *Genitalia*: ♀ 2nd valvulae (Figs. 22, 29) slightly broadened at or beyond midpoint, with distinct dorsal serrations; ♂ lat-

eral plates (Figs. 23) fused to pygofer; apex of aedeagus tentaculate (Fig. 24).

Range.—Chile, Venezuela.

Remarks.—As Evans (1961a) observed, *Holdgatiella* superficially resembles *Deiroideres*, differing chiefly in wing venation and morphology of the male and female genitalia. Evans placed *Holdgatiella* in the subfamily Centrotinae, while noting that the genus is closely related to the complex comprising Aetalionidae, Nicomiidae (now Membracidae: Nicomiinae), Biturritidae (now Aetalionidae: Biturritiinae), and the leafhopper subfamilies Ulopinae and Macropsinae. Linnavuori and DeLong (1978a) wrote, “*Holdgatiella*, an undoubted Mesozoic relic, evidently belongs to Membracidae as suggested by Evans, although it apparently has rather an isolated position within this family. Its relations to the other Membracidae remain open until a modern revision of the neotropical representatives of the family has been done.” Indeed, this genus was among seven membracid genera unplaced to subfamily in Deitz and Dietrich’s (1993a) reclassification of Membracoidea. The morphology-based phylogenetic analyses of Dietrich et al. (2001a) suggest that *Holdgatiella* is the sister group to Nicomiinae, and the authors noted that an expanded concept of Nicomiinae (to include *Holdgatiella* and other groups) might be warranted. In those analyses, *Holdgatiella* is closely allied with *Nicomia* and *Tolanina*, based primarily on forewing venation: vein M with three branches and vein R with four branches (only in *H. stria*, new species, but apparently the plesiomorphic condition). The tentaculate male aedeagus of *Holdgatiella*, however, sets it distinctly apart from these genera. Results from a separate morphology-based phylogenetic investigation of basal treehopper groups (Cryan et al. in press) agreed with the alliance of *Holdgatiella* with Nicomiinae. A more detailed analysis of relationships within Nicomiinae and related groups is underway (Albertson and Dietrich, personal communication).

KEY TO THE SPECIES
OF ADULT *HOLDGATIELLA*

1. Scutellum (Fig. 19) without mid-dorsal groove; metathoracic femur (Fig. 20) with ventral row of cucullate setae; forewing (Fig. 21) with 2 or 3 m-cu crossveins; frons with foliate lobes weakly developed (Fig. 18)
 *H. chepuensis* Evans
 — Scutellum (Fig. 26) with mid-dorsal groove; metathoracic femur (Fig. 27) without ventral cucullate setae; forewing (Fig. 28) with only 1 m-cu crossvein; frons with foliate lobes well developed (Fig. 25) *H. stria*, new species

Holdgatiella chepuensis Evans
(Figs. 18–24)

Holdgatiella chepuensis Evans 1962a: 516.

Type locality.—Chepu, Chile.

Diagnosis.—*Holdgatiella chepuensis* has a ventral row of cucullate setae on the metathoracic femur.

Adult.—*Dimensions* (mm): total length ♀ 6.5–7.0, ♂ 6.1–6.4; width between humeral angles ♀ 2.2–2.4, ♂ 2.1–2.2; pronotal length ♀ 1.2–1.4, ♂ 1.3–1.4; wing length ♀ 5.5–5.9, ♂ 5.2–5.4; width of head including eyes ♀ 2.4–2.6, ♂ 2.3–2.4. *Coloration*: ♀: face and body tan with dark brown markings, legs tan, forewing tan basally, hyaline apically; ♂: face and body fuscous with black markings, abdominal sternites yellow, abdominal tergites yellow with brown transverse stripes, legs fuscous dorsally, tan ventrally, forewing brown basally, anterior half of membranous area hyaline, posterior half brown. *Structure*: *Head*: face (Fig. 18) with weakly developed foliate lobes; postclypeus ovoid. *Thorax*: *Pronotum* (Fig. 19): humeral angles produced, blunt; median dorsal carina weak; posterior margin without triangular projections. *Pronotal surface sculpturing*: punctate; pits shallow, associated with a single short, apically curved seta. *Scutellum* (Fig. 19): slightly swollen basally, flattening to acuminate apex. *Legs* (Fig. 20): metathoracic femur with dorsal and ventral rows of cucullate setae (20–26 and 15–18 setae, respectively). *Forewing* (Fig. 21): basal $\frac{1}{3}$ – $\frac{1}{2}$ coriaceous; branching pattern of

vein R variable; 2 or 3 m-cu crossveins present, distal m-cu crossvein distad of first branch of vein M. *Genitalia*: ♀: 2nd valvulae (Fig. 22) abruptly broadened in distal $\frac{1}{3}$; dorsal ridge of broadened area weakly serrate. ♂: lateral plate (Fig. 23) fused to pygofer; styles (Fig. 24) elongate, ventrally curved to axe-like apical lobe; aedeagus (Fig. 24) L-shaped, anterior arm irregularly shaped, posterior arm slender; anterior face of posterior arm apically tentaculate (5 pairs of short, tentacle-like appendages).

Nymph.—Unknown.

Distribution.—Chile: Aucar [JWEC]; Cautin [JARC]; Chepu [NCSU]; Llanquihue [JARC]; Osorno [JARC].

Material examined.—Holotype not examined. Other specimens: 2 ♀ and 4 ♂ from JARC, 1 ♂ from JWEC, and 1 ♂ from NCSU.

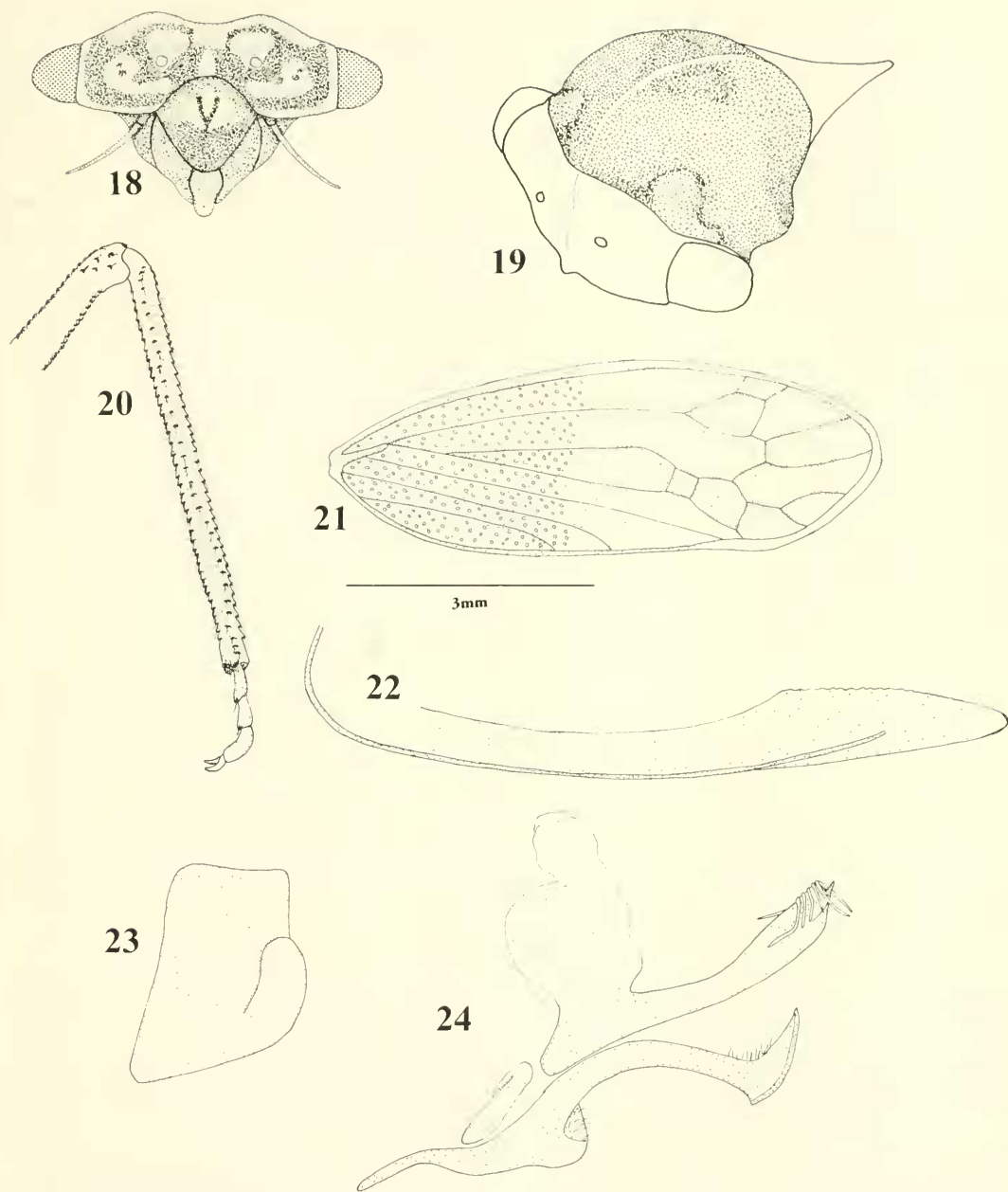
Remarks.—The aedeagal structure of this species differs greatly from that of other treehoppers. Not only are the apical lobes of the styles uniquely shaped, but also the presence of five pairs of apical appendages on the aedeagal corona sets *H. chepuensis* apart. Linnavuori and DeLong (1978a) illustrated various anatomical structures of *H. chepuensis*, including the hindwing, which appears nearly identical in venation to *Microcentrus* hindwings (Deitz 1975a, fig. 37c; Dietrich et al. 2001a, fig. 2B). The specific name “*chepuensis*” refers to the type locality, Chepu, Chile.

Holdgatiella stria Cryan and Deitz,
new species
(Figs. 25–29)

Type locality.—20 km SE of Azulita, Mérida, Venezuela.

Diagnosis.—*Holdgatiella stria* has the pronotum with posterolateral processes, the scutellum with a median dorsal groove, and the forewing with 1 m-cu crossvein.

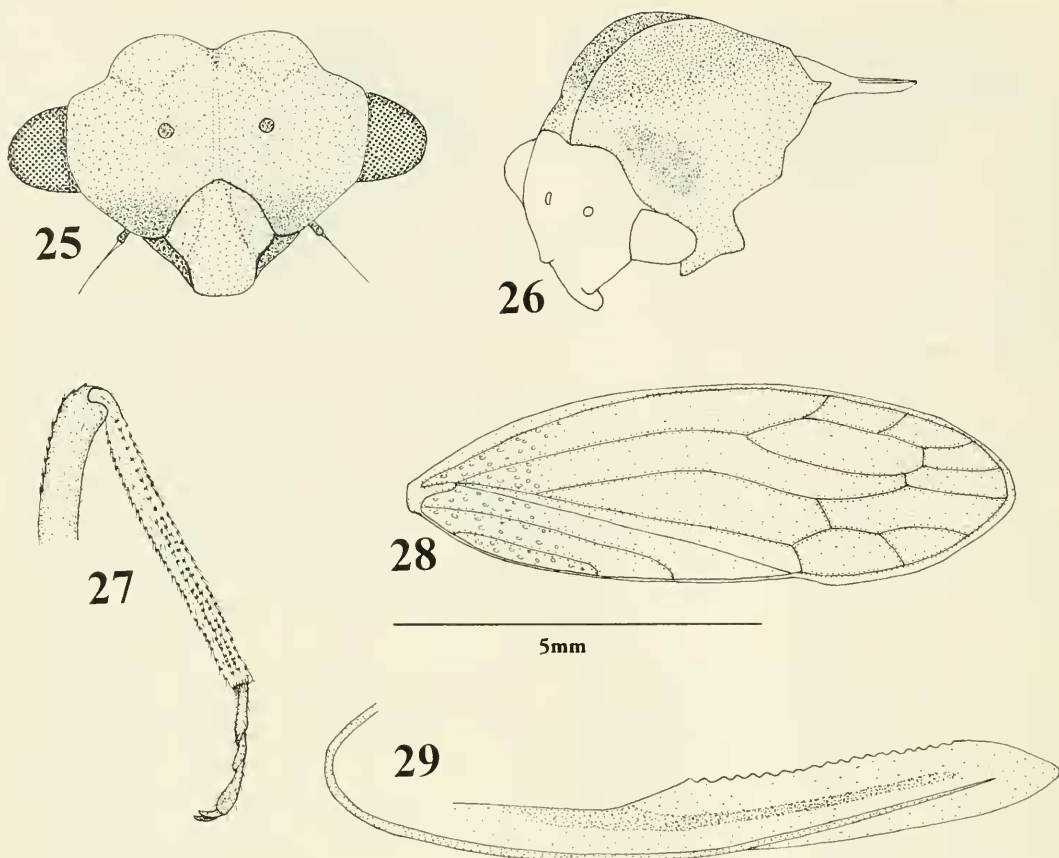
Adult ♀.—*Dimensions* (mm): total length 7.9; width between humeral angles 2.6; pronotal length 2.1; wing length 7.0; width of head including eyes 2.5. *Coloration*: face tan with fuscous punctures and



Figs. 18–24. *Holdgatiella chepuensis*. 18, Head, anterior aspect (face). 19, Head, pronotum, and scutellum, anterolateral aspect. 20, Left metathoracic femur, tibia, and tarsus, ablatral aspect. 21, Right forewing. 22, Female second valvulae, lateral aspect. 23, Male left lateral plate and pygofer, lateral aspect. 24, Male aedeagus and left style, lateral aspect (illustrated with connective tissue).

foliate lobes, body tan with dark markings, pronotum tan with brown metopidial crown, legs tan, forewing tan basally, hyaline apically. *Structure: Head: face* (Fig. 25) with well-developed foliate lobes; post-

clypeus weakly trilobed. *Thorax: Pronotum* (Fig. 26): humeral angles short, stout; median dorsal carina well developed; posterior margin with triangular projections on either side of scutellum. *Scutellum* (Fig.



Figs. 25–29. *Holdgatiella stria*. Structures of the holotype. 25, Head, anterior aspect (face). 26, Head, pronotum, and scutellum, anterolateral aspect. 27, Left metathoracic femur, tibia, and tarsus, ablatral aspect. 28, Right forewing. 29, Female second valvulae, lateral aspect.

26): slightly produced basally, flattening to acuminate apex, with median dorsal groove. *Legs* (Fig. 27): metathoracic femur with dorsal row of 15–18 cucullate setae; metathoracic tibia with paired cucullate setae in distal $\frac{1}{2}$ of row II. *Forewing* (Fig. 28): basal $\frac{1}{4}$ coriaceous; vein R with 4 branches (R_1, R_2, R_3, R_{4+5}); 1 m-cu crossvein present, distad of first branch of vein M. *Genitalia*: 2nd valvulae (Fig. 29) slightly broadened midway; dorsal ridge of distal $\frac{1}{2}$ serrate. δ : unknown.

Nymph.—Unknown.

Distribution.—Venezuela: Mérida [SHMC/USNM].

Material examined.—Holotype [♀] [SHMC, deposited on indefinite loan to USNM], with labels “VEN: Merida, 20

km/SE Azulita, La/Carbonera 27.VII-/3.VIII.89 S&J Peck,” “ ♀ ,” “*Holdgatiella* sp./det. S. McKamey 1991,” and “HOLOTYPE/*Holdgatiella/stria*/Cryan & Deitz.”

Remarks.—Although the scutellum is not emarginate apically, the presence of a median dorsal groove suggests that the ancestors of *H. stria* had a posterior pronotal process that was secondarily lost. The specific name “*stria*” is Latin for “furrow” or “groove,” referring to the median dorsal groove of the scutellum.

Genus *Togotolanía* Cryan and Deitz, new genus

Type species.—*Togotolanía longicornis*, new species.

Diagnosis.—*Togotolanía* has the follow-

ing unique combination of characters: head with large dorsal projections, pronotum with a median horn, and forewings each with 3 r-m and 1 m-cu crossveins.

Adult.—*Dimensions* (mm): total length (from head to apex of forewings at rest) 6.4–7.2. *Structure: Head:* dorsal cranial projections large, either pyramiform (Fig. 30) or emarginate (Fig. 35); ocelli on or above centro-ocular line. *Thorax: Pronotum* (Figs. 31, 36): metopidium elevated; supraocular callosities indistinct; posterior process lacking, suprahumeral horns absent or represented by low carinae at base of median dorsal horn. *Scutellum* (Figs. 31, 36): short with swollen base, flattening to acuminate apex. *Legs* (Fig. 32): metathoracic tibia with enlarged setal rows I, II, and III, all with reduced cucullate setae. *Forewing* (Figs. 33, 37): 3 r-m crossveins present; vein R_{4+5} fused to R basad of fork of R_1 and R_{2+3} ; 1 m-cu crossvein present, distad of fork of vein M. *Hindwing:* venation essentially identical to *Microcentrus* hindwing venation as illustrated by Deitz (1975a, fig. 37c) and Dietrich et al. (2001, fig. 2B). *Genitalia:* ♀ 2nd valvulae (Fig. 34) broadened at midpoint; ♂ lateral plates (Fig. 38) free, lacking apical hook; styles (Fig. 39) slender, with apical hook; aedeagus (Fig. 39) U-shaped, with posterior arm tapering sharply at apex.

Range.—Dominican Republic, Guadeloupe.

Remarks.—Included in the phylogenetic analysis of Dietrich et al. (2001a) as “New Genus T”, *Togotolanía* was placed in a largely unresolved lineage basal to the clade comprising Nicomiinae + Centronodinae + Centronodinae. Results of a separate morphology-based analysis (Cryan et al. in press) were concordant, with *Togotolanía* placed at the base of a lineage comprising *Holdgatiella*, *Tolanía*, and Centronodini. Although we here leave *Togotolanía* unplaced in the family Membracidae, we acknowledge that this genus is probably allied with Nicomiinae. The generic name “*Togotolanía*” translates as “cloaked *To-*

lanía” and refers to the hoodlike pronotal structure. It is formed from “*toga*” [Latin] and “*tolanía*” [origin unknown], joined by the vowel “o” for euphony (Brown 1956).

KEY TO THE SPECIES
OF ADULT *TOGOTOLANIA*

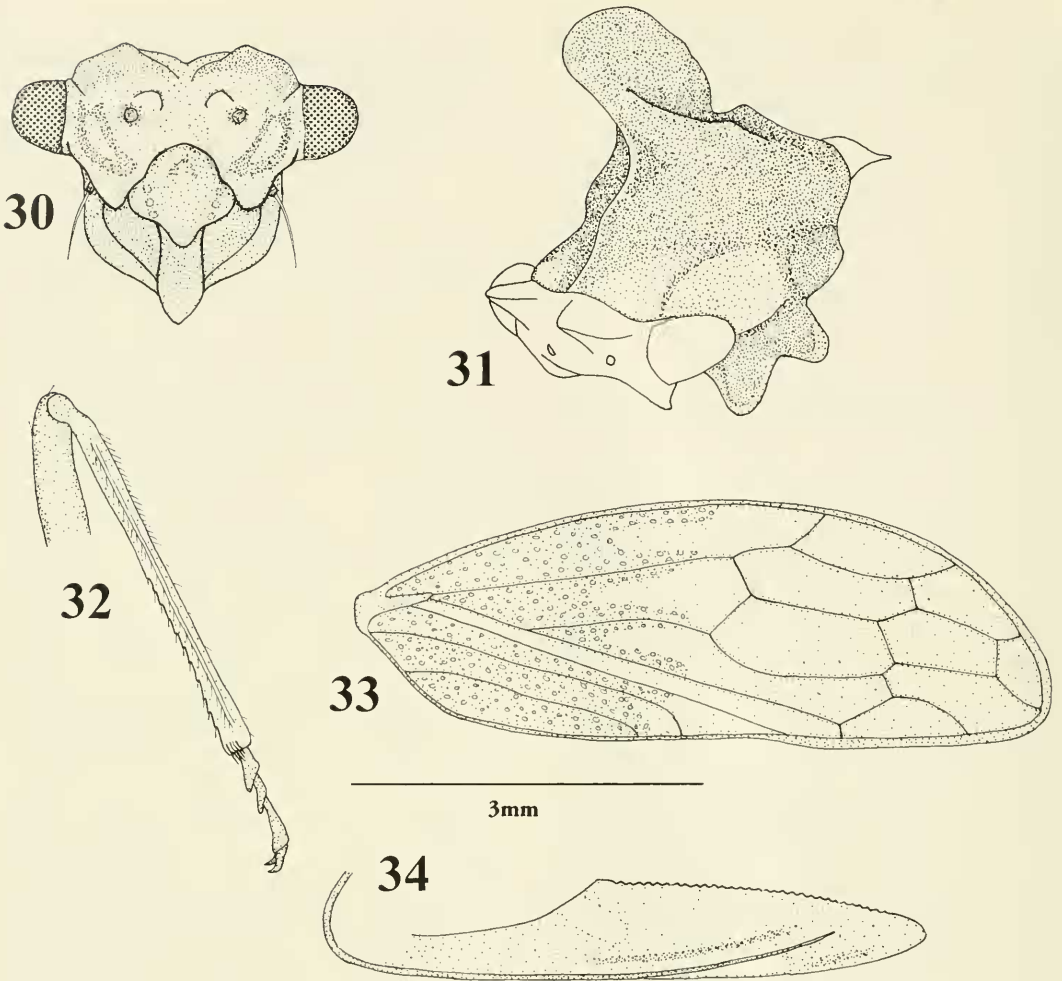
1. Median pronotal horn (Fig. 31) large, laterally compressed; head (Figs. 30–31) with pyramiform dorsal projections; forewing (Fig. 33) with crossvein r-m₂ distad of fork of vein M *T. longicornia*, new species
- Median pronotal horn (Fig. 36) small, not laterally compressed; head (Figs. 35–36) with emarginate dorsal projections; forewing (Fig. 37) with crossvein r-m₂ basad of fork of vein M *T. brachycornia*, new species

***Togotolanía longicornia* Cryan and Deitz,
new species
(Figs. 30–34)**

Type locality.—2 km east of Boca Chica, Dominican Republic.

Diagnosis.—*Togotolanía longicornia* is easily recognized by its large, median, anterior pronotal horn; the pronotum is uniformly black.

Adult ♀.—*Dimensions* (mm): total length 6.4; width between humeral angles 1.9; pronotal length 1.6; wing length 5.1; width of head including eyes 1.9. *Coloration:* face tan with dark brown ovate markings; body fuscous with pronotum black; forewing brown with dark venation; legs brown. *Structure: Head:* face (Fig. 30) strongly sulcate between pyramiform dorsal projections; postclypeus weakly trilobed, each lateral lobe with 3 small callosities; foliate lobes strongly developed. *Thorax: Pronotum* (Fig. 31): humeral angles well developed, blunt; median dorsal horn laterally compressed; suprahumeral horns reduced to low carinae at base of median horn. *Scutellum* (Fig. 31): apex acuminate, lacking median dorsal groove. *Legs* (Fig. 32): metathoracic femur with 1 dorsal cucullate seta; metathoracic tibia with weakly cucullate setae in rows I, II, and III. *Forewing* (Fig. 33): r-m₂ and r-m₃ distad of fork of vein M. *Genitalia:* 2nd valvulae (Fig. 34) broadened at midpoint, tapering to apex;



Figs. 30–34. *Togotolania longicorna*. Structures of the holotype. 30. Head, anterior aspect (face). 31. Head, pronotum, and scutellum, anterolateral aspect. 32. Left metathoracic femur, tibia, and tarsus, ablatral aspect. 33. Right forewing. 34. Female second valvulae, lateral aspect.

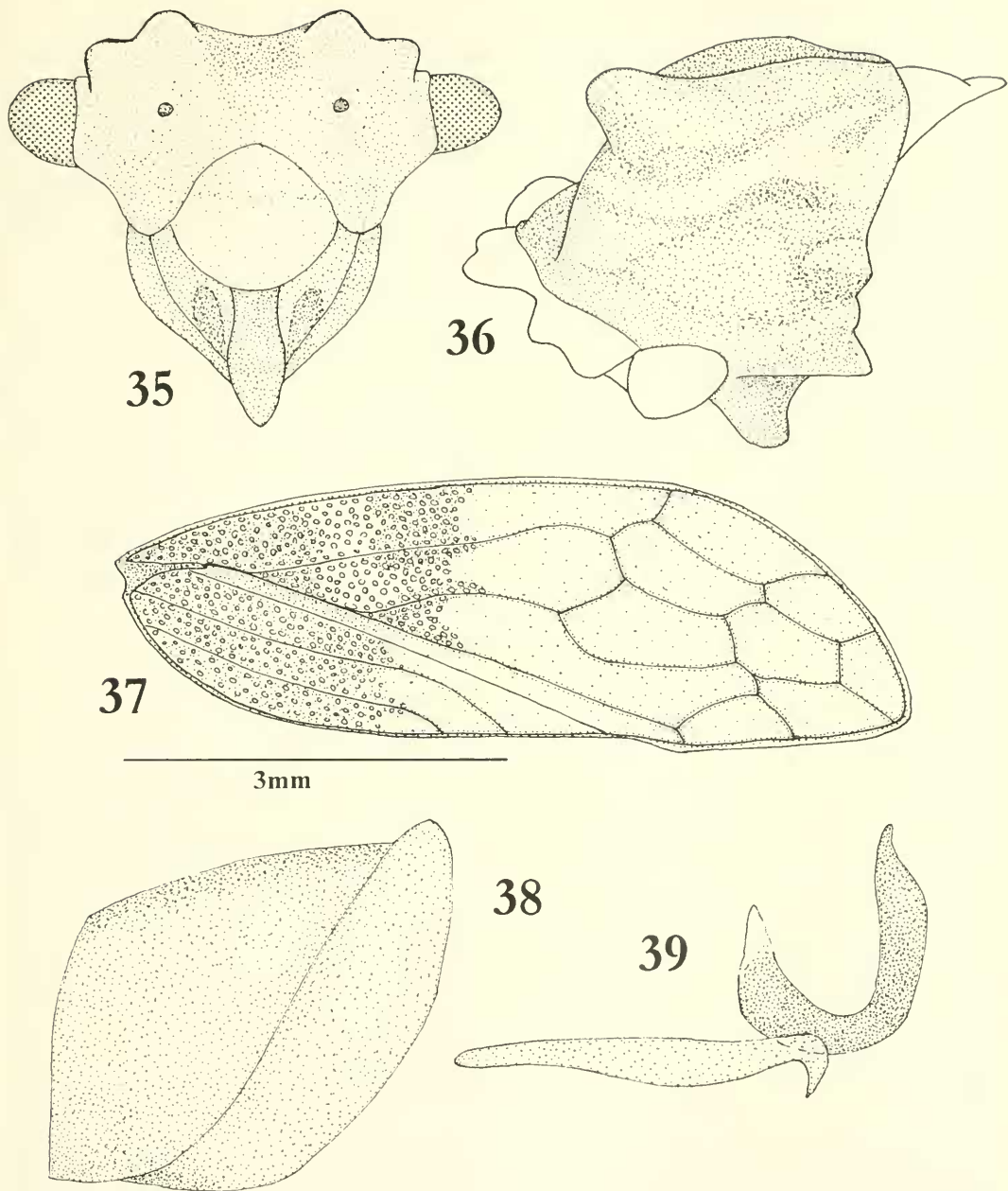
dorsal ridge of broadened area serrate. ♂: unknown.

Nymph.—Unknown.

Distribution.—Dominican Republic [SHMC/USNM].

Material examined.—Holotype [♀, dissected] [SHMC, on indefinite loan to USNM] with labels “DOM. REP. Dis. Nac.,/2 km. E. Boca Chica/August 11, 1979/C.W. O’Brien,” “VOUCHER SPECIMEN/Cuticular Hydrocarbon/Analysis Study/Jason R. Cryan, 1995,” “HOLOTYPE/*Togotolanialongicornal*/Cryan & Deitz,” and “SHM.”

Remarks.—*Togotolania longicorna*, described from a single female specimen, is unique in its large, median dorsal horn on the crest of the pronotal metopidium. The suprahumeral carinae are located at the base of this horn; in some other treehopper groups with a dorsal pronotal elongation, the suprahumeral horns or carinae are at or near the apex (for example, the genus *Lycoderes* Germar; see Cryan and Deitz 1999b: fig. 2). The Latin specific name “*longicorna*” translates as “long horned,” referring to the median anterior pronotal horn.



Figs. 35–39. *Togotolania brachycorna*. Structures of the holotype. 35, Head, anterior aspect (face). 36, Head, pronotum, and scutellum, anterolateral aspect. 37, Right forewing. 38, Male left lateral plate and pygofer, lateral aspect. 39, Male aedeagus and left style, lateral aspect.

***Togotolania brachycorna* Cryan and Deitz, new species**
(Figs. 35–39)

Type locality.—Riv. Corossol, Guadeloupe.

Diagnosis.—The median, anterior pronotal horn of *Togotolania brachycorna* is short and weakly developed; the pronotum is mottled brown and tan, with a pale stripe encircling the median horn.

Adult ♂.—*Dimensions* (mm): total length 7.2; width between humeral angles 2.3; pronotal length 1.9; wing length 5.6; width of head including eyes 2.2. *Coloration*: face, body, pronotum, and legs mottled brown and tan; pronotum with pale strip encircling median horn; basal $\frac{1}{2}$ and venation of forewing dark brown. *Structure*: *Head*: face (Figs. 35–36) strongly sulcate between large, emarginate dorsal projections; postclypeus unilobed; foliate lobes rounded. *Thorax*: *Pronotum* (Fig. 36): humeral angles well developed, blunt; median dorsal horn weakly developed; suprahumeral horns absent. *Scutellum* (Fig. 36): apex acuminate, lacking median dorsal groove. *Legs*: metathoracic femur with 1 dorsal cucullate seta; metathoracic tibia with minute cucullate setae in rows I, II, and III. *Forewing* (Fig. 37): r-m₁ and r-m₂ basad of fork of vein M. *Genitalia*: lateral plates (Fig. 38) large, free, lacking apical hook; styles (Fig. 39) slender, hooked apically; aedeagus (Fig. 39) strongly U-shaped, with posterior arm tapered and lacking denticles on anterior face. ♀: unknown.

Nymph.—Unknown.

Distribution.—Guadeloupe [CIRAD/MNHN].

Material examined.—Holotype [♂, dissected, with hindwings and 1 leg mounted beneath specimen] [CIRAD, deposited at MNHN] with labels "GUADELOUPE/Forêt, PETIT-BOURG/Riv. Corossol/20-X-1962/J. Bonfils," "3," and "HOLOTYPE/*Togotolanialbrachycorna*/Cryan & Deitz."

Remarks.—*Togotolanialbrachycorna*, described from a single male specimen, has a much shorter median pronotal horn relative to its congener (described above). The suprahumeral horns are lacking, and the pronotal coloration differs greatly from that of *T. longicornis*. Based on morphological variation and geographical separation, we believe the possibility is remote that *T. brachycorna* is the male of *T. longicornis*. The Latin specific name "*brachycorna*" trans-

lates as "short horned," referring to the median anterior pronotal horn.

DISCUSSION AND SUMMARY

The genus *Deiroderes* (with three species) is potentially allied to *Antillotolanis* within the subfamily Stegaspidae, although tribal association is unclear. Despite some similarities with the genera *Melizoderes* and *Llanquihuea* (family Melizoderidae; Linnavuori and DeLong 1978a, Deitz and Dietrich 1993a), *Holdgatiella* and *Togotolanis* (each with two species) are apparently among the basal lineages within Membracidae, probably allied with the subfamily Nicomiinae (Dietrich et al. 2001a; Cryan et al. in press). Further studies may confirm that one or two new family group taxa are needed to accommodate these treehoppers.

ACKNOWLEDGMENTS

We are grateful to R. L. Blinn, H. H. Neunzig, B. M. Wiegmann, and C. H. Dietrich, who offered many helpful suggestions, and to S. H. McKamey for bringing new taxa to our attention. G. Kuschel kindly provided etymological assistance regarding "*Deiroderes*." For lending specimens, we are indebted to: the late J. A. Ramos (JARC); the late J. W. Evans (JWEC); R. L. Blinn (NCSU); S. H. McKamey (SHMC); the late R. C. Froeshner (USNM); and K. G. A. Hamilton (CNCI).

This work is based in part on portions of the 1995 thesis submitted by J.R.C. in partial fulfillment of his M.S. degree in entomology (North Carolina State University). The material is based upon work supported in part by the North Carolina Agricultural Research Service (NCSU, Raleigh, North Carolina) and by the National Science Foundation Grants DEB-9815867 and DEB-9978026. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the North Carolina Agricultural Research Service or the National Science Foundation.

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